

INTROGRESSIVE HYBRIDIZATION BETWEEN NATIVE CUTTHROAT TROUT AND INTRODUCED RAINBOW TROUT

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Abstract. Introgressive hybridization threatens the persistence of several species of native salmonids in the western United States, but little is known about the factors influencing the establishment and maintenance of introgressed populations. We examined the occurrence of introgressive hybridization in westslope cutthroat (*Oncorhynchus clarki lewisi*) and rainbow trout (*O. mykiss*) populations in relation to physical characteristics of streams, trout density estimates, and the distance from stocking source. Trout were sampled from 80 stream sites in the Clearwater River Basin, Idaho, USA, and tissues from individual trout were analyzed to detect hybridization using noncoding sequences of nuclear DNA. We found a broad zone of hybridization detected at 64% of the sampled sites. The presence and degree of introgression was negatively related to elevation and positively related to stream width in our logistic regression model. Stream elevation and size likely influence hydrologic and thermal regimes. An interaction between the life history characteristics of the native and nonnative trout with these hydrologic and thermal stream gradients could explain the invasion success of rainbow trout and hence, the extent of the hybrid zone. Alternatively, the influence of elevation and stream width could be the result of habitat selection by the parental species, thereby reducing the opportunity for hybridization. Understanding the relationship between abiotic factors and introgressive hybridization will assist fisheries managers when evaluating the potential threat of introgression in different stream habitats and applying the necessary management actions to conserve the native cutthroat trout genotypes across broad landscapes.

Key words: cutthroat trout; hybrid zone; introgression; nonnative introductions; nuclear DNA; *Oncorhynchus clarki*; *Oncorhynchus mykiss*; rainbow trout.

INTRODUCTION

Hybridization with introduced species threatens many species of invertebrates, fish, birds, and mammals (Rhymer and Simberloff 1996). Hybridization may affect a native population through lost reproductive opportunity and/or introgression (Allendorf et al. 2001). When hybrids are fertile and readily backcross with the parental taxa, genetic mixing can be extensive. This introgressive hybridization alters the genetic composition of the native population and can result in extinction of the native genotypes (Rhymer and Simberloff 1996). However, the biotic and abiotic interactions maintaining introgressed populations of native and nonnative species are not well understood. Moreover, introgressive hybridization can spread widely and become an uncontrollable problem for scientists trying to protect native species (Allendorf et al. 2001).

Nonnative species and strains of trout are often introduced to enhance sport or commercial fisheries and

frequently result in the establishment of self-sustaining populations. For example, in the Columbia River basin, rainbow trout (*Oncorhynchus mykiss*) are the most widely introduced and distributed nonnative salmonid (Thurrow et al. 1997). Nonnative rainbow trout readily hybridize with native cutthroat trout (*O. clarki*) resulting in fertile hybrids. This introgressive hybridization is thought to be the greatest threat to the conservation of several subspecies of native cutthroat trout (Allendorf and Leary 1988). Of the 14 subspecies of cutthroat trout native to western North America (Behnke 1992), one is extinct, four are protected under the Endangered Species Act, and the rest are designated species of concern by various state and federal agencies. Although habitat alteration and fragmentation have contributed to the declines of most of the subspecies, hybridization and competition with nonnative trout are also a widespread problem (Allendorf and Leary 1988, Shepard et al. 1997, Kruse et al. 2000). Despite the threat of introgression, some fish management agencies continue to stock nonnative rainbow trout in waters supporting populations of native cutthroat trout.

Historically, westslope cutthroat trout (*O. clarki lewisi*) were distributed in northern Idaho, western Mon-

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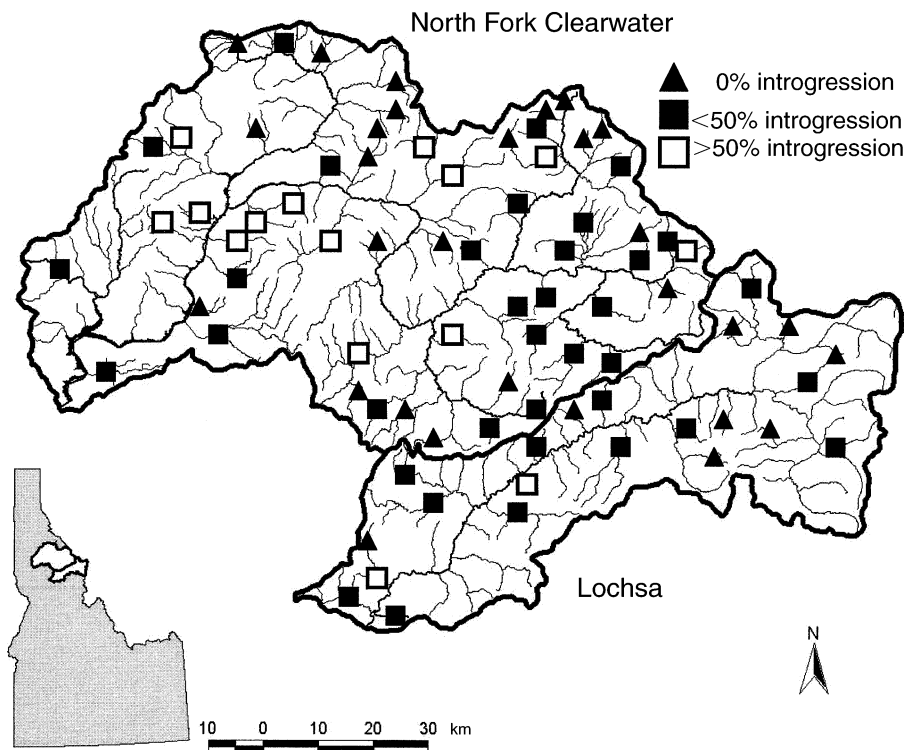


FIG. 1. Locations of sample sites in the North Fork Clearwater ($n = 58$) and Lochsa ($n = 22$) river basins, Idaho, USA.

tana, and portions of Canada with several disjunct, isolated populations in Washington and Oregon (Behnke 1992). A small portion of their native range in Idaho overlaps that of native anadromous rainbow trout (*O. mykiss gairdneri*). Although widespread, the westslope cutthroat populations remain strong in <22% of their historical range due to habitat degradation and the impacts of nonnative fishes (Lee et al. 1997). Nonetheless, the remaining populations represent a wide diversity of genetic structure, which suggests a high potential for local adaptations and increases the importance of conservation of these genotypes (Allendorf and Leary 1988, Behnke 1992).

Currently, little is known about the factors that influence the establishment and maintenance of introgressed populations of salmonids. This information is crucial for developing effective strategies for the conservation of native genotypes. Therefore, we studied the distribution of introgressive hybridization in two subbasins of the Clearwater River, Idaho, USA, where nonnative rainbow trout have been stocked with native rainbow and westslope cutthroat trout for >50 yr. The objectives of our study were: (1) to determine the distribution of introgression between rainbow trout and westslope cutthroat trout and (2) to relate this distribution to physical and biotic stream characteristics and stocking locations.

STUDY AREA

Study areas were located in two adjacent subbasins of the Clearwater River, the North Fork Clearwater and Lochsa basins, in north-central Idaho (Fig. 1). The North Fork Clearwater and Lochsa river basins share a north-south ridgeline and are 6320 and 3021 km², respectively. Land in the study area is primarily managed for timber harvest by private, state, and federal agencies. However, approximately one-third of the study area is managed as wilderness (Quigley and Arbelbide 1997). The annual peak flow in both basins occurs during spring snowmelt in late May, and low flows occur during late summer (August–September) and winter (December–January). Sites sampled during the study ranged in elevation from 512 to 1828 m and daytime summer water temperatures were 8–21°C.

The North Fork Clearwater and Lochsa river basins historically had substantial runs of native steelhead and other anadromous species (Thurrow et al. 1997). Anadromous access was blocked from the North Fork Clearwater River in 1972 after the completion of Dworshak Dam, located 3.2 km upstream from the mouth of the river. Dworshak Reservoir inundates up to 86.2 km of the lower river and tributaries. When native anadromous rainbow trout were extirpated from the North Fork Clearwater basin, it was thought that westslope cutthroat trout would increase in abundance to fill the

TABLE 1. Summary of the locations of rainbow trout stocking in the North Fork Clearwater and Lochsa river basins, Idaho, USA, based on stocking records at the Idaho Department of Fish and Game (Lewiston, Boise, and Coeur d'Alene, Idaho), U.S. Forest Service (Clearwater National Forest, Orofino, Idaho), and U.S. Fish and Wildlife Service (Ahsahka, Idaho) from 1940 to 2000.

Location	No. sites	Elevation (m)	Total biomass (kg/yr)	Mean fish size (trout/kg)	Stocking (yr)		Range of years stocked
					Single	Multiple	
North Fork Clearwater Basin							
Dworshak Reservoir	>7	486	2250–39 150	5–132	2	24	1972–2000
Mainstem river	>4	607–975	31–2085	2–438	3	3	1940–1981
Stream tributaries	6	625–1158	225–455	6–12	2	6	1940–1979
Headwater lakes	28	1646–2060	9000–13 500	8–8800	3	26	1940–2000
Lochsa Basin							
Mainstem river	>4	607–975	91–8861	3–995	0	40	1940–1990
Stream tributaries	17	594–1676	2–7484	2–2030	8	13	1940–1985
Headwater lakes	27	1658–2134	5–27	8–4000	3	25	1942–2000

Notes: Listed above are: general location of stocking by habitat type; number of sites where rainbow trout were stocked in each habitat type; range in elevation of stocked sites; range in total biomass of rainbow trout stocked per year; range in the mean recorded size of rainbow trout stocked; the number of years with only one stocking event; the number of years with more than one stocking event; and the range of years that rainbow trout stocking was reported in the records.

vacant niche (Moffitt and Bjornn 1984). However, comparative studies did not detect an increase in abundance of cutthroat trout after the exclusion of anadromous rainbow trout. These studies detected a decline in rainbow trout abundances during the initial few years after exclusion, after which rainbow trout abundances began to increase (Moffitt and Bjornn 1984, Hunt and Bjornn 1991). Although nonnative rainbow trout were stocked into the North Fork Clearwater basin before the construction of Dworshak Dam, the resulting fisheries mitigation program for the dam and reservoir substantially increased the number of rainbow trout stocked annually in the basin (Table 1). In the Lochsa Basin, anadromous salmon and rainbow trout continue to persist even though eight dams impede passage between the Lochsa River and the Pacific Ocean. These naturally reproducing anadromous runs, however, have been declining for several decades (Thurrow et al. 1997).

STOCKING HISTORY

Various species and strains of trout and salmon have been stocked into the study area for >50 yr. Our search included electronic databases (1969–present) and handwritten records from the Idaho Department of Fish and Game (IDFG; Lewiston, Coeur d'Alene, and Boise, Idaho), U.S. Forest Service (USFS; Clearwater National Forest, Orofino, Idaho), and U.S. Fish and Wildlife Service (USFWS; Fisheries Resource Office, Ahsahka, Idaho). The oldest stocking records found were dated 1940, but it is likely that stocking activities began earlier in the century similar to other regions in the U.S. (Behnke 1992, Fausch et al. 2001). Six strains of rainbow trout have been reportedly stocked in the mainstem, tributaries, and headwater lakes within the North Fork Clearwater and Lochsa basins, but most records do not indicate which strain was stocked. Chinook salmon (*O. tshawytscha*), kokanee salmon (*O. nerka*), smallmouth bass (*Micropterus dolomieu*), bull trout

(*Salvelinus confluentus*), brook trout (*S. fontinalis*), grayling (*Thymallus arcticus*), golden trout (*O. mykiss aquabonita*), Yellowstone cutthroat trout (*O. clarki bouveri*), and cutthroat \times rainbow trout hybrids also were stocked in the study area.

All sites with records of rainbow trout stocking were included in our analysis regardless of stocking date. The oldest records found were sporadic, incomplete, and may not reflect actual stocking effort. We did not include locations where anadromous rainbow trout (steelhead) or cutthroat trout (westslope or unspecified subspecies) were released. Steelhead stocking locations were not included because we assumed that they would have less potential for interaction with westslope cutthroat trout. Although hybridization with hatchery steelhead trout may occur, including these sites in our analysis would not alter the results because nonnative rainbow trout were stocked at many of the same locations. It was unclear whether cutthroat trout stocked in the 1940s and 1950s were westslope or Yellowstone cutthroat trout. When specified, recorded stocking of Yellowstone cutthroat trout and cutthroat \times rainbow trout hybrids coincided with locations of rainbow trout stocking. The mainstem North Fork Clearwater and Lochsa rivers were stocked in several locations along the stream to spread the fish over the stream length. These locations likely changed over time as access points (such as boat ramps or bridges) were developed or decommissioned. Similarly, Dworshak Reservoir was stocked in several locations that changed from year to year. From 1985 to 1991, rainbow trout were released continuously from a barge traveling from the dam to the upstream end of the reservoir (R. Roseberg, *personal communication*). The size of rainbow trout released, number of releases per year, and total mass released each year was variable (Table 1). Multiple stocking events of all sizes of trout within a single year

TABLE 2. Characteristics of sites in the Lochsa and North Fork Clearwater river basins.

Variable	Abbreviation	Lochsa		North Fork Clearwater	
		Mean (SD)	Range	Mean (SD)	Range
Distance to stocking source (km)	Distance	4.7 (4.6)	0.0–18.1	9.9 (7.2)	0.0–30.7
Elevation (m)	Elevation	1233.4 (379.8)	512.1–1828.8	1104.3 (287.0)	542.5–1633.7
Stocking elevation (m)	Stock elevation	1062.2 (379.4)	594.4–1956.8	932.6 (460.6)	485.8–1978.8
Gradient (%)	Gradient	5.7 (3.8)	1.0–16.0	4.7 (3.0)	1.5–14.0
Width (m)	Width	4.6 (2.2)	1.4–9.4	5.5 (2.5)	1.8–13.7
Depth (m)		0.2 (0.1)	0.1–0.3	0.2 (0.1)	0.1–0.4
Pool maximum depth (m)	Pool depth	1.4 (1.4)	0.0–4.0	1.8 (1.4)	0.0–8.0
Instream cover (%)	%Cover	43 (29)	5–90	32 (18)	5–80
Streamside cover (%)		19 (22)	0–90	22 (19)	0–90
Streambed fines (%)	%Fines	29 (23)	1–100	24 (17)	3–84
<i>Oncorhynchus</i> density (no./100 m ²)	Density	52.3 (31.0)	5.1–104.0	36.2 (31.6)	0.3–117.0

Note: Variables with abbreviations were uncorrelated and were included in candidate logit models for predicting westslope cutthroat trout and westslope × rainbow hybrid trout presence.

also were common, particularly between 1940 and 1960. Releases of trout weighing 100–150 g each were most common, and all stocking occurred during the summer months (June–September).

METHODS

Trout, tissue samples, and habitat data were collected from 58 sites in the North Fork Clearwater basin and from 22 sites in the Lochsa basin from July through October 1997–1999 (Fig. 1). Access of high elevation sites and seasonal high flows during spring snowmelt limited sampling to the summer months. We initially used fisheries survey data to identify streams where cutthroat and rainbow trout were present (USFS, Clearwater National Forest, Orofino, Idaho, *unpublished data*; IDFG, Lewiston and Coeur d'Alene, Idaho, *unpublished data*; see summary in Weigel [1997]). After eliminating streams that did not support populations of *Oncorhynchus* sp. trout, we stratified all potential sampling reaches by major tributary and stream order within each tributary. We attempted to sample an equal number of sites within each major tributary and each stream order to ensure broad spatial coverage and to represent the wide variety of habitats in each basin (Table 2). When possible, we sampled near the middle of the selected stream segment; however, the local terrain prevented access in some locations. In these cases, we sampled as close as possible to the selected stream segment.

Trout collection and density estimates

Sampling consisted of blocking off 50 m long sites with 4 mm mesh seines secured to the stream bottom and banks with rocks to prevent fish movement. Trout were sampled using three upstream passes with a backpack electrofisher (Smith-Root model 15D; Smith-Root, Vancouver, Washington, USA) powered with a generator (Honda EX350; distributed by Smith-Root). Electrofishing was done with a standard DC pulse rate of 60–80 Hz with 800–1000 V. All trout were identified and total length was measured to the nearest millimeter

as defined in Anderson and Gutreuter (1983). The first 20 *Oncorhynchus* sp. trout captured were usually sampled for genetic analysis but we also included all sizes of fish captured in the total sample to minimize the possibility of sampling siblings. A small piece of the pelvic or caudal fin was excised and preserved in 95% ethanol. The adipose fin was removed as a permanent mark to prevent resampling individuals that may have traveled to different sites.

All cutthroat, rainbow, and hybrid trout were combined for abundance estimates at each site to avoid inaccurate visual identifications. Age-0 trout were not included in the density estimates because they had not yet emerged at the beginning of the sampling period. Removal estimators, traditionally used in fishery research, could not provide reliable estimates of fish abundance because they are biased by factors such as fish species and size (Buttiker 1992, Anderson 1995) and the physical characteristics of the area sampled (Kennedy and Strange 1981, Riley et al. 1993). Therefore, we used sampling efficiency models to adjust trout length-frequency data for the effects of physical stream characteristics and fish body size on capture efficiency. Three-pass backpack electrofisher sampling efficiency was estimated using the following sampling efficiency model for *Oncorhynchus* sp. in streams

$$\pi = \{1 + \exp[-(-0.8890 - 0.4167\text{crx} + 0.0047\text{con} + 1.2809\text{size}_2 + 1.4601\text{size}_3)]\}^{-1}$$

where π = predicted efficiency as a fraction, crx is the mean stream cross sectional area (in square meters), con is the stream conductivity (in microsiemens per centimeter), size₂ is coded as 1 when total fish length (TL) is between 99 and 199 mm and 0 otherwise, and size₃ is 1 when TL > 199 mm and 0 otherwise (R. Thurow, *unpublished data*). Catch data then were adjusted using the techniques in Bayley and Dowling (1993) and were standardized to the wetted surface area of the sample site to obtain density estimates.

Habitat measurements and distance to stocking

To identify the ecological clines at each site, we measured several physical habitat characteristics that have been reported to influence the distribution and abundance of stream-dwelling trout (Gard and Flittner 1974, Bozek and Hubert 1992, Dunham et al. 1999). Elevation (in meters) of each site was estimated from a 1:24 000 USGS topographic map. Percentage of gradient was measured over the site with a hand-held clinometer and stadia rod. Percentage of the area covered by instream and streamside cover was visually estimated over the site. Instream cover was defined as areas created by boulders, aquatic vegetation, wood, or turbulence providing visual isolation of trout from other fish and potential predators. Streamside cover was overhanging riparian vegetation or undercut bank within 0.5 m of the water surface. Pool habitat was identified as slow water habitat with channel scour as defined in Arend (1999). Maximum depth (in meters) was measured for each pool in the site. Wetted width (in meters) and substrate composition (as percentages) were measured on transects at 10-m intervals along the site. Percentage of stream bed area covered by fine substrate <8 mm was visually estimated along each transect. Three depth measurements (in meters) were also taken at one-quarter intervals across the stream channel at each transect. Width, depth, and the percentage of fine sediments then were averaged for each site using the transect data. Using identical measurement procedures, Thurow et al. (2001) found these measures to be repeatable and estimated with at least 30% precision.

Distance to the nearest stocking location (in kilometers of stream length) of any strain of rainbow trout was measured from topographic maps. We used the most accessible location such as a bridge, road, or trail present at the time of release as the best estimate of the stocking location. Because the mainstem Lochsa and North Fork Clearwater rivers had multiple undocumented stocking locations and were accessible by road throughout their length, we calculated distance to the mainstem river when this was the closest location. Locations of upstream migration barriers documented during stream surveys were used to determine the nearest accessible source of stocked trout (USFS, Clearwater National Forest, Orofino, Idaho, *unpublished data*; Panhandle National Forest, St. Maries, Idaho, *unpublished data*; IDFG, Lewiston, Idaho, *unpublished data*). For example, if a waterfall blocked access to a site from downstream, the closest stocking location upstream was used. We assumed stocked trout could move downstream over potential barriers, such as waterfalls. Stocked rainbow trout had upstream or downstream access to all sites.

Genetic analysis

Hybrids were identified using Paired Interspersed Nuclear Element (PINEs)-polymerase chain reaction

(PCR; Spruell et al. 1999). This technique amplifies multiple nuclear DNA fragments that are flanked by interspersed elements of known sequence from each PCR and has been used to detect hybrids in several salmonid fishes (Spruell et al. 2001; Kanda et al. 2002) including rainbow trout and cutthroat trout (Smithwick 2000). To identify informative fragments, pure (non-hybridized) populations were identified throughout the native range of each species using protein electrophoresis. Individuals were collected from at least 25 of these known pure populations for each species and screened using PINEs to identify fragments that amplify exclusively in cutthroat trout and others amplifying exclusively in rainbow trout (see Smithwick [2000] for details). Mendelian inheritance of these species-specific fragments makes this method useful when detecting hybrids (Greene and Seeb 1997, Spruell et al. 1999).

Briefly, DNA was extracted using the PureGene kit (Gentra, Minneapolis, Minnesota, USA) following the manufacturer's directions. The PCR amplification of PINE products was performed under the following conditions. The PCRs contained ~25 ng of genomic DNA, 1 μ L 10 \times Perkin-Elmer PCR buffer (Perkin-Elmer, Foster City, California, USA), 4.5 mmol/L MgCl₂, 0.2 mmol/L of each dNTP, 5.0 pmol of primer, and 0.5 U Taq. Reactions were completed in an MJ Research PTC-100 thermal cycler (MJ Research, Watertown, Massachusetts, USA) using the following profile: 3 min at 95°C, followed by 30 cycles of 91°C for 1 min, 60°C for 1 min, 72°C for 2.5 min, then 72°C for an additional 2.5 min. Products were stored at 12°C until electrophoretic analysis was completed. Amplified products were size fractionated on a 4.5% denaturing polyacrylamide gel for 75 min at 65 W. The DNA fragments were visualized using an Hitachi FMBIO-100 fluorescent imager (Hitachi, South San Francisco, California, USA).

The genetic composition of trout at each site was estimated based on the presence or absence of informative fragments in all individuals from that site. Individuals were initially screened with a minimum of two PINE primer combinations. The identity of all individuals from a sampling location was then used to classify sites as either hybridized, putatively pure west-slope cutthroat trout, or putatively pure rainbow trout. However, hybrid swarms, in which all individuals are hybrids, will often contain individuals that do not appear to be hybrids based on a limited number of genetic markers (Allendorf et al. 2001). Therefore, populations in which there was no evidence of genetic material from rainbow trout were analyzed using another pair of primers to provide additional statistical confidence that the populations were not hybridized. We calculated the probability of failing to detect hybrids by assuming these dominant markers are completely diagnostic, are unlinked, and are inherited in a simple Mendelian manner (Spruell et al. 1999). Using up to 16 markers and

a sample size of 20 individuals per site, we achieved a 95% confidence that hybridization would be detected in a population of westslope cutthroat trout that contains >1% rainbow trout genes.

The final classification of each population was based on the percentage of individuals with only westslope cutthroat markers, only rainbow trout markers, or markers indicative of both species (hybrids). Due to the dominant nature of PINE markers, it is not possible to estimate allelic frequencies without assuming the population is in Hardy-Weinberg equilibrium. This assumption is probably frequently violated in hybridized populations. Therefore, we used the percentage of hybrid individuals rather than allelic frequencies as our measure of the extent to which each population was hybridized (described below).

Statistical analysis

Sites were divided into three categories based on the level of introgression detected in the genetic analysis from each site. Sites where only markers for westslope cutthroat trout were detected in all individuals were classified as 0% introgression. All other sites had at least one individual that had diagnostic markers indicative of both cutthroat and rainbow trout. We separated these hybrid sites into two groups, greater than and less than 50% introgression, based on the percentage of hybrid individuals at each site.

We used a multinomial logit model (Agresti 1990) to examine the relationships between site characteristics and the degree of introgression. A multinomial logit model (hereafter, logit model) differs from the more familiar binary logistic regression model in that the probabilities of more than two categorical responses are estimated simultaneously based on several predictors. The logit model is also more robust than and generally outperforms traditional categorical data analysis techniques, such as discriminant analysis (Press and Wilson 1978). To aid in interpretation of model coefficients, 0% introgression was used as the baseline response category. Pearson correlations were calculated for all pairs of predictor variables (i.e., site characteristics) prior to analyses. To avoid multicollinearity, a subset of eight uncorrelated predictor variables ($r^2 < 0.15$) was selected for inclusion in our candidate models (Table 2).

We used the information-theoretic approach, described by Burnham and Anderson (1998), to evaluate the relative plausibility of the logit models. The subset of uncorrelated site characteristics was used to construct the global model containing all of the predictors. From this model, we constructed a subset of 31 candidate models that we considered biologically relevant containing various combinations of the predictors from the global model. We assessed the fit of each of the candidate models using Akaike's Information Criteria (AIC; Akaike 1973) corrected for a small sample bias (AIC_c; Hurvich and Tsai 1989). Akaike's Information

Criteria is an entropy-based measure used to compare candidate models describing the same data (Burnham and Anderson 1998), with the best fitting model having the lowest AIC_c. The relative plausibility of each candidate model was assessed by calculating Akaike weights (w_i) as described in Burnham and Anderson (1998). The most plausible candidate model has the greatest Akaike weight (range 0 to 1).

To incorporate model-selection uncertainty, we computed model-averaged estimates of the logit model coefficients and their standard errors as described by Buckland et al. (1997) and Burnham and Anderson (1998). Briefly, the estimated coefficients (i.e., model parameters) and their corresponding standard errors from each candidate model were weighted by their associated Akaike weights and summed across the different models resulting in a composite model. All inferences were based on the composite models. The ratio of the weights for two candidate models also can be used to assess the relative evidence for one model over another (Burnham and Anderson 1998). Model-averaged coefficients and standard errors were only calculated for the predictor variables that occurred in one or more candidate models with weights within 10% of the largest weight. The relative importance of individual predictor variables also was estimated as the sum of Akaike weights for candidate models in which each predictor occurred (Burnham and Anderson 1998).

To allow for ease of interpretation, we estimated standardized model-averaged coefficients and scaled odds ratios for each predictor variable in the composite model (Hosmer and Lemeshow 1989). The odds ratio scalars corresponded to what we believed to be biologically relevant unit changes in the predictors (e.g., a 100-m change in elevation). The precision of each predictor was estimated by computing 95% confidence intervals for the scaled odds ratios (see Hosmer and Lemeshow 1989). Confidence intervals that contained 1 indicated inconclusive results because we could not determine the nature of the relationship (i.e., whether positive or negative) due to imprecision in parameter estimates (Thompson and Lee 2000).

Goodness-of-fit was assessed for the global model via Andrews' (1988) omnibus χ^2 test, a multinomial generalization of the more familiar Hosmer-Lemeshow test. Dependence among sites within basins was examined by conducting an analysis of variance (ANOVA) on the residuals from the global model. Significant differences between basins would indicate dependence among sites within basins (Snijders and Bosker 1999).

RESULTS

Cutthroat \times rainbow trout hybrids were distributed in a broad hybrid zone in the study area (Fig. 1, Table 3). Introgression was detected at 64% of the sites sampled. The frequency of the level of introgression among these sites showed a bimodal distribution (Fig. 2). Sites with a greater proportion of the individuals with west-

TABLE 3. Total number of sites (n) and percentage of sites in the North Fork Clearwater and Lochsa river basins with 0%, <50%, and >50% introgression detected using genetic analysis.

Basin	n	Percentage of sites, by level of introgression		
		0%	<50%	>50%
North Fork Clearwater	58	37	41	22
Lochsa	22	36	55	9

slope cutthroat trout genotypes (i.e., <50% introgression) were more numerous. In addition to the 80 sites analyzed, we detected two sites with populations of rainbow trout (no introgression) and one site with introgressed Yellowstone cutthroat trout. Although we could not examine interannual variation in the level of introgression, we assumed that it was minimal and that our three groups of classification were relatively robust to interannual variation.

The Andrews omnibus goodness-of-fit test indicated that the fit for the global logit model was adequate ($\chi^2 = 20.0$, $df = 18$, $P = 0.33$). The ANOVA of residuals indicated no detectable dependence among sites within basins ($F = 0.08$, $P = 0.77$). Consequently, we assumed that the logit model fit was also adequate for the candidate models (i.e., the subsets of the global model).

The most plausible logit model of genetic introgression contained elevation and mean stream width and was 2.5 times more likely than the next best approximating model, which contained elevation only (Table 4). The composite model contained these two predictors and their interaction, distance to stocking source, and gradient (Table 5). Importance weights for elevation and mean stream width were more than five times greater than those of other predictors in the composite model and indicated that there was strong evidence for these two predictors (Table 5). Elevation appeared to have the greatest influence on (i.e., largest standardized coefficient), and was negatively related to, the presence

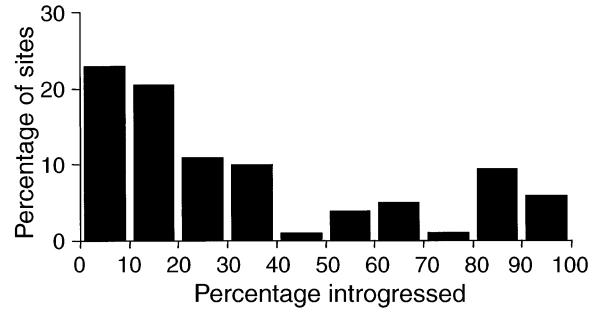


FIG. 2. Percentage of sites by the level of introgression, expressed as the percentage of hybrid individuals detected at the introgressed sites ($n = 51$). Introgressed sites were classified into two groups (<50% and >50% introgression) based on the bimodal distribution suggested.

of introgressed populations. Scaled odds ratios suggested that populations with >50% introgression were 2.2 (1/0.464) times less likely and populations with <50% introgression were 1.4 times less likely to occur than pure populations with every 100-m increase in elevation. Mean stream width appeared to be positively related to the presence of introgressed populations (Table 5). However, the coefficients were relatively imprecise, and the confidence intervals on the scaled odds ratios were wide and contained one, so the precise nature of the relationship could not be determined. Evidence was inconclusive for the remaining predictors.

Model predictions based on the composite model (Table 5) for streams with small (2.5 m) and medium (7.5 m) mean wetted width indicated that the probability of occurrence of introgressed populations decreased with increased elevation at both stream sizes (Fig. 3). At low elevations (<700 m), our model predicts that the presence of <50% and >50% introgressed populations are equally likely in small streams, whereas in wider streams introgressed populations >50% are most likely to occur at this elevation. At high elevations (>1500 m), pure populations of west-

TABLE 4. Summary of model selection statistics for the set of candidate models (i) for predicting westslope cutthroat trout and westslope cutthroat \times rainbow hybrid trout presence.

Candidate model	K	$-2 \ln \mathcal{L}$	AIC_c	ΔAIC_c	w_i	Percentage of maximum w_i
Elevation, Width	7	131.08	146.63	0.00	0.440	100.0
Elevation	5	137.67	148.48	1.85	0.175	39.8
Elevation, Width, Elevation \times Width	9	129.19	149.77	3.13	0.092	20.9
Elevation, Gradient, Width	9	129.29	149.86	3.23	0.088	19.9
Distance, Elevation, Width	9	130.09	150.66	4.03	0.059	13.3
Elevation, Width, Stock elevation	9	130.91	151.49	4.85	0.039	8.8
Distance, Elevation	7	136.88	152.43	5.80	0.024	5.5
Distance, Elevation, Width, Elevation \times Width	11	127.32	153.20	6.57	0.016	3.7
Distance, Elevation, Gradient	9	132.98	153.55	6.92	0.014	3.1
Elevation, Width, %Cover, %Fines	11	127.75	153.63	7.00	0.013	3.0

Notes: Akaike weights (w_i) are interpreted as relative plausibility of candidate models. Other column heads are defined as follows: K , number of parameters; \mathcal{L} , likelihood; AIC_c , Akaike Information Criteria with small sample bias adjustment.

TABLE 5. Model-averaged results and odds ratios for composite multinomial logit model of westslope cutthroat trout introgression.

Model parameter	Estimated coefficient (1 SE)	Standardized coefficient	Odds ratio unit change	Estimated odds ratio	95% CI for odds ratio		Importance weight
					Upper	Lower	
Less than 50% introgressed							
Intercept	3.874 (2.045)	0.518					
Elevation	−0.003 (0.002)	−0.983	100 m	0.708	0.905	0.526	1.000
Mean width	0.045 (0.282)	0.378	3 m	1.145	6.004	0.218	0.765
Distance to stocking source	0.049 (0.076)	0.230	10 km	1.626	7.271	0.364	0.153
Gradient	−0.132 (0.098)	−0.429	3%	0.674	1.198	0.379	0.112
Elevation × width	<0.001 (0.001)	0.525		1.221	1.655	0.901	0.108
Greater than 50% introgressed							
Intercept	5.833 (2.685)	−1.272					
Elevation	−0.008 (0.002)	−2.311	100 m	0.464	0.741	0.290	1.000
Mean width	0.267 (0.349)	1.019	3 m	2.227	17.311	0.286	0.765
Distance to stocking source	0.144 (0.176)	0.461	10 m	4.238	134.410	0.134	0.153
Gradient	−0.117 (0.143)	−0.382	3%	0.703	1.633	0.303	0.112
Elevation × width	<0.001 (0.001)	0.705		1.308	1.989	0.861	0.108

Notes: Coefficients should be interpreted relative to pure westslope cutthroat trout (the baseline). The importance weights are calculated using the Akaike weights from the individuals and are the same for both logit models (<50% and >50% introgression).

slope cutthroat were most likely to occur in small streams, whereas in wider streams, introgressed populations <50% were most likely to occur. Introgressed populations <50% also were most likely to occur at

intermediate elevations (800–1400 m) for both small and moderate-sized streams.

We were concerned that the influence of elevation could have been confounded with the other predictors in the composite model. An examination of pairwise plots indicated no discernable relationship between mean width and elevation, nor gradient and elevation (Fig. 4). The plot of distance to stocking source and elevation indicated there were few sites at low elevations with long distances to stocking. Hence, the effect of elevation and distance to stocking could not be differentiated at lower elevations (<700 m). However, distance to stocking appeared to have little influence on introgression at higher elevations (Fig. 4).

DISCUSSION

We found a broad zone of westslope cutthroat trout and rainbow trout hybridization at low to intermediate elevations in the Clearwater River basin, which was similar to that described for Apache trout (*O. apache*) in Arizona (Carmichael et al. 1993) and Yellowstone cutthroat trout in northwestern Wyoming (Kruse et al. 2000). Hybrid zones occur naturally, but tend to be relatively narrow areas located between adjacent populations of the native parental species (Barton and Hewitt 1985). In contrast, our study and that of Carmichael et al. (1993) found that stocking of nonnative trout tends to establish broad hybrid zones where only the native parental species is present outside of the area of hybridization, and populations of the nonnative parental species are absent or rare. Thus, hybridization with introduced species appears to create a different type of hybrid zone than those of native species. This suggests that mechanisms that presumably minimized natural hybridization between westslope cutthroat trout

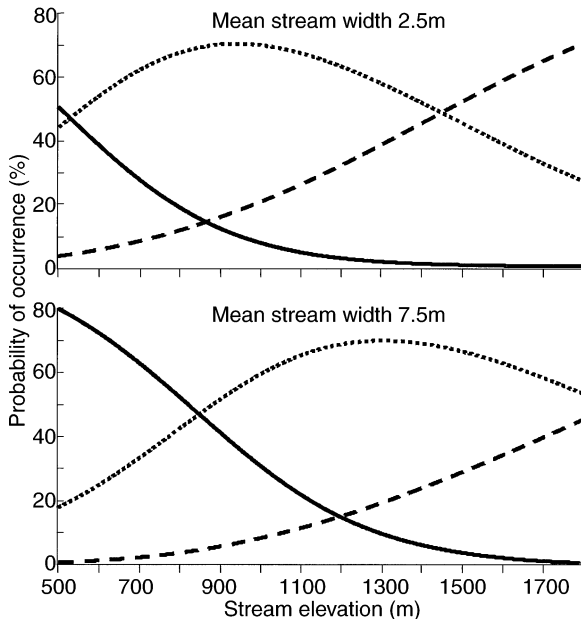


FIG. 3. Estimated probability of occurrence for putatively pure westslope cutthroat populations (dashed line), populations with <50% hybrid individuals (dotted line), and those with >50% hybrid individuals (solid line) in narrow and wide streams at various elevations in the North Fork Clearwater and Lochsa river basins. Predictions are based on the composite multinomial logit model (see Table 5) and calculated for mean distance to stocking (8.4 km) and stream gradient (5.0%) across basins.

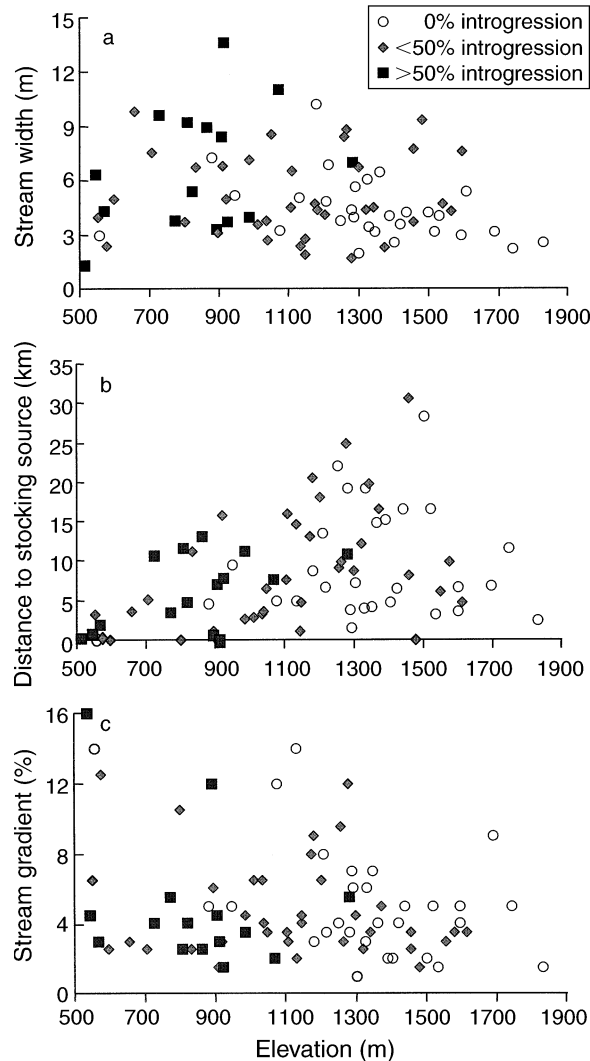


FIG. 4. Relationship between elevation and (a) mean stream width, (b) distance to stocking source, and (c) stream gradient for sites with cutthroat populations with 0%, <50%, and >50% introgression.

and native rainbow trout are probably missing in non-native rainbow trout.

Spatial and temporal reproductive segregation is believed to be one of the most important factors reducing the incidence of hybridization in closely related salmonid species (Leary et al. 1995). Zoogeography and fossil records suggest that native rainbow trout inhabited the Clearwater Basin prior to westslope cutthroat trout, which are thought to have colonized 20 000–60 000 yr ago (Behnke 1992). Thus, we assume that the establishment and maintenance of westslope cutthroat trout populations in the presence of native anadromous rainbow trout required the existence or development of reproductive isolation mechanisms. Indeed, Hanson (1977) reported that westslope cutthroat trout and native anadromous rainbow trout exhibited strong

spatial segregation in tributaries of the Lochsa River, with cutthroat restricted to smaller tributary or headwater habitat and native rainbow trout in the lower stream reaches. Conversely, the overlap in habitat use of nonnative rainbow trout and westslope cutthroat trout (Pratt 1985) and the diversity of spawning times expressed among the numerous hatchery strains of rainbow trout (Williams et al. 1997, Robison et al. 1999) increase the potential for hybridization. We hypothesize that nonnative rainbow trout are largely responsible for the broad hybrid zones observed in the Clearwater basin.

Interestingly, the distribution of the frequency of introgressed genotypes suggested a bimodal pattern. Bimodality has been described for individuals within populations of hybrids of various taxa (Jiggins and Mallet 2000) and is thought to result from selection against the intermediate genotypes or segregation between the species. Our observation of the frequency of introgressed genotypes could be influenced by losses in fitness of certain hybrid crosses (Allendorf and Leary 1988, Leary et al. 1995), habitat selection by the parental taxa (Magee et al. 1996, Henderson et al. 2000), or patterns related to the migration of the introduced rainbow trout genes in the study area.

The level of introgression detected in our study was most strongly related to elevation and stream size. This relationship is similar to many other studies of the distribution of native and nonnative trout, where native trout are frequently found in smaller, higher elevation stream habitats (e.g., Fausch 1989, Bozek and Hubert 1992, Dunham et al. 1999, Weigel and Sorensen 2001). This pattern could not be attributed to access limitations (e.g., barriers) because rainbow trout had access to all sample locations and stocking occurred over a range of elevations throughout our study area. Rather, we believe that these patterns may be determined by an interaction between local abiotic variables (such as hydrologic or temperature regimes) and the physiological or life history characteristics of nonnative trout and hybrids.

Hydrologic regimes are thought to have a significant influence on the success of invading fish species (Moyle and Light 1996a, Fausch et al. 2001). Stream discharge has been found to reduce salmonid reproduction by scouring eggs from redds (gravel nests) and displacing postemergent fry (Seegrist and Gard 1972, Heggnes and Traaen 1988, Lisle and Lewis 1992). Rainbow trout fry typically emerge from the gravel between April and June (Fausch et al. 2001), whereas native westslope cutthroat trout typically spawn in late May and early June (Magee et al. 1996, Downs et al. 1997) and emerge in July through September. In the Clearwater Basin, peak flows tend to occur mid-March to late April at lower elevations (below 900–1000 m) due to earlier snowmelt runoff and the greater frequency of rain-on-snow events, whereas peak flows at higher elevations tend to occur late May to mid-June

(N. Gerhardt, *personal communication*). With this hydrologic pattern, eggs and postemergent fry of rainbow trout would likely experience greater mortality during the later peak flows in higher elevation streams, effectively reducing recruitment and increasing the proportion of pure fish at higher elevations.

Thermal regime also influences the reproductive success and survival of salmonids. Cold summer temperatures can delay spawning and prolong egg incubation in spring spawning rainbow trout and cutthroat trout (Hubert et al. 1994, Stonecipher et al. 1994). Cold summer temperatures also reduce the length of the growing season, which decreases salmonid fry growth and consequently, overwinter survival (Hunt 1969, Smith and Griffith 1994, Meyer and Griffith 1997). Higher elevation streams in the Clearwater basin generally have colder summer temperatures and shorter growing seasons (Quigley and Arbelbide 1997). In contrast, wider streams generally receive greater amounts of solar input and tend to be slightly warmer than smaller streams at similar elevations (Poole and Berman 2001). Thus, colder temperatures and shorter growing seasons in the smaller, higher elevation streams could have reduced the ability of the nonnative rainbow or hybrid trout to survive or successfully reproduce, thereby excluding them from these areas.

Alternatively, the influence of elevation and stream width on the distribution of introgression may simply be the result of habitat selection by parental species. Cutthroat trout generally spawn in smaller streams and at higher elevations than native and nonnative rainbow trout and cutthroat \times rainbow trout hybrids (Magee et al. 1996, Henderson et al. 2000), reducing the opportunity for hybridization. However, in larger (mainstem) streams spawning areas for nonnative rainbow trout, native cutthroat trout, and their hybrids overlap considerably (Henderson et al. 2000), which may explain the greater potential for introgression in wider streams at higher elevations.

Distance to stocking was only weakly related to hybridization in our study area. Possible reasons for a lack of relationship include: (1) stocking records were frequently incomplete; (2) the public may have moved fish between locations creating unrecorded introductions; (3) stocked trout may have moved long distances from the location of release; and (4) stocked trout failed to establish reproducing populations at many stocking locations. Most stocking in the study area occurred in mainstem rivers, headwater lakes, and reservoirs. These habitats often do not provide suitable spawning habitat (cf. Northcote 1997) so stocked trout may have moved to new habitats and hybridized with the native trout. The establishment of nonnative populations also is influenced by the duration, magnitude, and timing of introductions (Moyle and Light 1996b). However, these relationships could not be examined using our data because stocking events were highly variable over time and the records were incomplete.

Although most lower elevation sites in our study area were close to stocking locations, there was little evidence of a relationship between introgression, elevation, and stocking location. Introgressed and pure populations of cutthroat trout at moderate to high elevations were both near and far from recorded stocking locations. The highest elevation stocking locations were in headwater lakes. The movement of nonnative trout from headwater lakes has been documented in several drainages in Idaho and Montana (Allendorf and Leary 1988, Leary et al. 1995, Adams et al. 2001), but stocking in headwater lakes was not strongly associated with introgression in our study. We detected introgression at only two of nine sites where headwater lakes were the closest stocking location of rainbow trout. Many headwater lakes were historically fishless and may not provide suitable spawning or rearing habitat.

Management implications

The distinct distribution pattern of introgression in westslope cutthroat trout populations in the Clearwater basin has several implications for management and sampling of introgressed populations of trout. Our data suggest that biological factors, rather than stocking practices, may be responsible for the observed distribution pattern. Biological barriers to introgression, such as habitat selection, assortative mating, and losses in fitness, have been found in several hybridized species of native interior trout (e.g., Dowling and Childs 1992, Leary et al. 1995, Henderson et al. 2000). Further understanding and identification of these barriers limiting gene exchange are essential to the management and conservation of native trout populations (Dowling and Childs 1992) and would allow managers to perform risk analyses of the potential for invasion of nonnative trout or introgression in different stream habitats. These tools would be useful when determining the need for various management actions, such as man-made barriers often used to protect cutthroat trout populations from invasion by nonnative trout (Kruse et al. 2001).

Population declines and extirpations of native cutthroat trout occur more often in larger, low elevation streams and often result in isolated and fragmented populations of genetically pure cutthroat trout (Dunham et al. 1997, 1999, Kershner et al. 1997, Shepard et al. 1997, Kruse et al. 2000). Currently, genetically pure westslope cutthroat trout populations are present only in $\sim 25\%$ of the stream habitat the North Fork Clearwater and Lochsa basins, and many of these are restricted to smaller, higher elevation streams. These high elevation populations could play a critical role in the genetic recovery of introgressed populations by contributing pure westslope cutthroat trout to populations in lower elevation habitats. Thus, we believe that managers should focus efforts on protecting these areas, expanding the pure populations, and maintaining connectivity among habitats to ensure the long-term

persistence of native westslope cutthroat trout populations and the preservation of their genotypes.

Currently, natural resource management agencies in western North America are developing strategies to classify populations of cutthroat trout based on the level of introgression (e.g., Utah Division of Wildlife 2000). Our data indicate that the level of introgression can vary widely within localized stream basins, and a large number of sites may be required to accurately describe the genetic status of cutthroat trout in a basin. Without careful sampling design, the risk of genetic misidentification is high, which could result in the unintentional destruction of native genotypes. Unfortunately, management programs frequently try to define introgressed populations for entire streams based on tissue samples collected from a single location or several grab samples dispersed over an entire length of stream ($n = 30$ individuals). We recommend that sufficient sampling of trout from several locations within a stream be tested for introgression to ensure $>95\%$ confidence of detecting introgression $>1\%$.

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